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THE ORIGIN AND EVOLUTION OF LIFE ON THE EARTH

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LECTURE II PART II

EVOLUTION OF THE FISHES

FOLLOWING the pro-fishes of Odrovician time (p. 508) the great group of fishes begins its evolution with (*A*) active, free-swimming, double pointed types of fusiform shape, adapted to rapid motion through the water and to predaceous habits in pursuit of swift-moving prey. From this type there radiated many others: (*B*) the deep, narrow-bodied fishes of relatively slow movements, frequenting the middle depths of the waters; (*D*) the swift-moving, elongate types which increasingly depended upon lateral motions of the body for propulsion and thus tended to lose the lateral fins and finally to assume an elongate, eel shape entirely finless; (*C*) other bottom-living forms in which the body became laterally flattened, the head very large relatively and covered with protective dermal armature, the movements of the animals very slow.

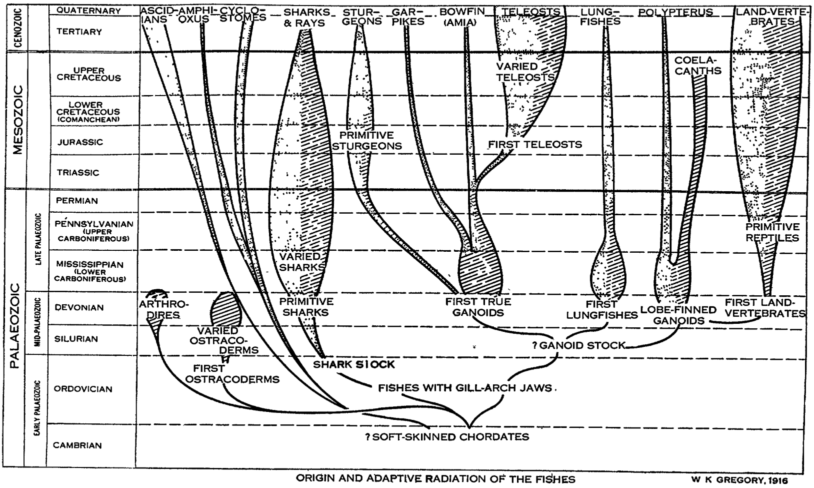

FIG. 9*a*. ORIGIN AND ADAPTIVE RADIATION OF THE FISHES SHOWING THE NOW EXTINCT SILURO-DEVONIAN GROUPS, the Ostracoderms and Arthrodires, in relation to the surviving lampreys (Cyclostomes), sharks, and rays (Elasmobranchs), sturgeons, garpikes, bowfins (Ganoids), bony fishes (Teleosts), primitive and recent lung-fishes (Dipnoi), and finally the fringe-finned Ganoids (Crossopterygii) from the cartilaginous fins of which the fore and hind limbs of the first land-living vertebrates (Tetrapoda) were derived. Dotted areas represent groups which still exist. Hatched areas represent extinct groups. Prepared for the author by Wm. K. Gregory.

Smith Woodward[6] has traced similar radiations of body form in the historic evolution of each of the great groups of fishes.

The importance of this law of form radiation is greatly enhanced when we find it repeated successively among the aquatic Amphibia, Reptilia and Mammalia as one of the invariable effects of the *coordination of the mechanism of motion with that of offense and defense.*

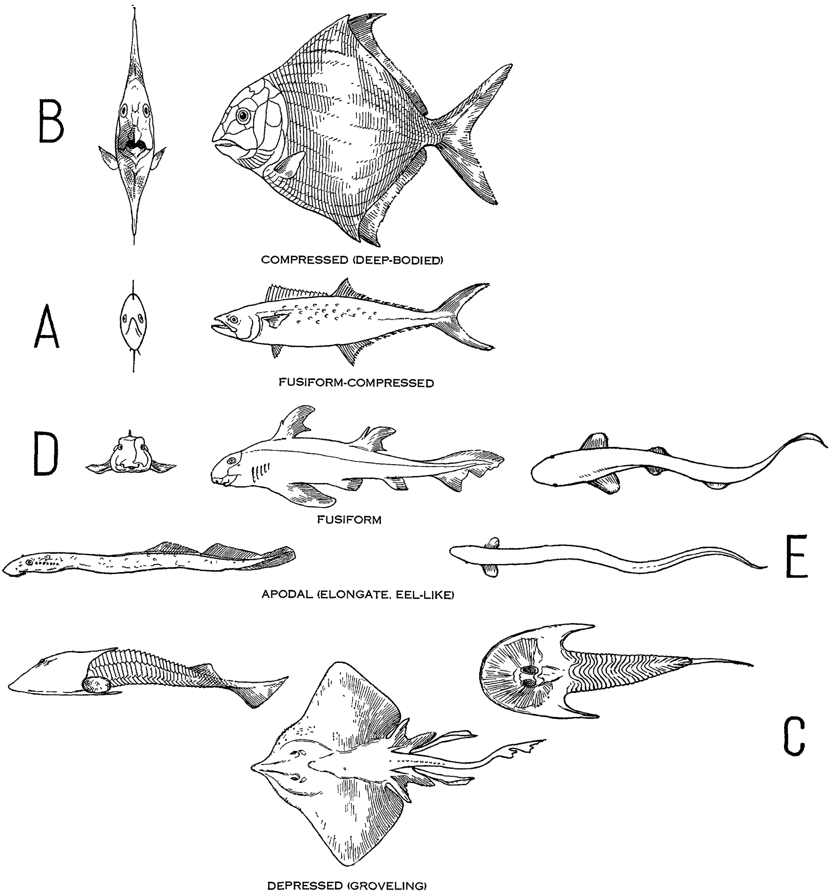

FIG. 9*b*. THE FIVE PRINCIPAL TYPES OF BODY FORM IN FISHES, beginning with (*A*) the swift-moving, compressed, fusiform types which pass, on the one hand, into (*B*) the compressed, slow-moving, deep-bodied types, and, on the other, into (*C*) laterally depressed, round, bottom-dwelling, slow-moving types, also into (*D*) elongate, swift-moving, fusiform types which grade into (*E*) the eel-like and swift-moving, bottom-living types without lateral fins. These five types of body form in fishes independently arise over and over again in the various groups of this Order. Partially parallel forms also appear among the Amphibia, Reptilia, and Mammalia. Prepared for the author by Wm. K. Gregory and Erwin S. Christman.

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[6] Smith Woodward, A., "The Use of Fossil Fishes in Stratigraphical Geology," *Proc. Geol. Soc. of London*, Vol. LXXI., Pt. 1, 1915, pp. lxii–lxxv.

In each of these four or five great radiations of form, from the swift-moving to the bottom- or ground-living, slow, armored types, there is usually an increase of bodily size, also an increase of specialization, the maximum in both being reached just before the period of extinction arrives.

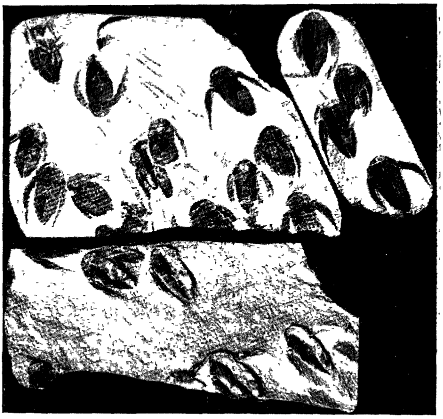

Fig. 10. Armored, Bottom-living Ostracoderm Type, *Bothriolepis*, from the Upper Devonian of Canada, with chitinous armature and a pair of anterior appendages analogous to those in Eurypterids. This cluster of animals was undoubtedly buried simultaneously while headed against the current either in search for food or for purposes of respiration. After Patten, *op. cit.*

The Ordovician Ostracoderms are very little known. The Upper Silurian Ostracoderms enjoyed a wide distribution in Europe and America. They include both the fusiform free-swimming type (*Birkenia*) and the depressed ray-like types (*Lanarkia*, etc.). They apparently had not yet acquired cartilaginous lower jaws and appear to be in a lower stage of evolution than the true fishes. The armature is arranged in shield and plate form in *Palæaspis*, from the Upper Silurian Salina time of Schuchert, where we obtain our first glimpse of North American land life in the presence of the oldest known air-breathing animals, the scorpion spiders, and also the first known land plants. There are many indications of an arid climate. In Upper Silurian time the Ostracoderms reach the slow, armored, bottom-living stage of evolution, as typified in the Pteraspidians and Cephalaspidians, which were widely distributed in Europe, in America, and possibly in the Antarctic regions, as indicated by recent explorations there. Belonging to a *very distinct order* or subclass (Antiarchi) are certain armored Devonian forms (*Bothriolepis, Pterichthys*, etc.), which possessed a pair of jointed lateral appendages. Propelled by a pair of appendages attached to the anterior portion of the body; some of these animals (*Bothriolepis*) present analogies to the eurypterids (Merostomata, or Arachnida).

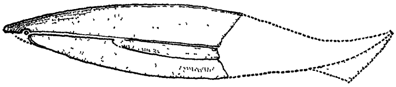

Fig. 11. The *Palæaspis* of Claypole as Restored by Dean.

In the freshwaters of the Lower Devonian have been discovered the ancestors of the heavily armored fishes known as the Arthrodira, a group of uncertain relationships. They have many characters in common with *Bothriolepis* (joint-neck, dermal jaws, carapace and plastron, paired appendages (*Acanthaspis*)). Dean, Hussakof and others regard the balance in favor of relationship with the stem of the Antiarchi (*Bothriolepis*). In the Middle Devonian (the Cleveland shales of Ohio) they attain the formidable size shown in the species *Dinichthys intermedius*. Like the Ostracoderms these animals are not central or in the main lines of fish evolution but represent collateral lines which early attained a very high degree of specialization followed by extinction.

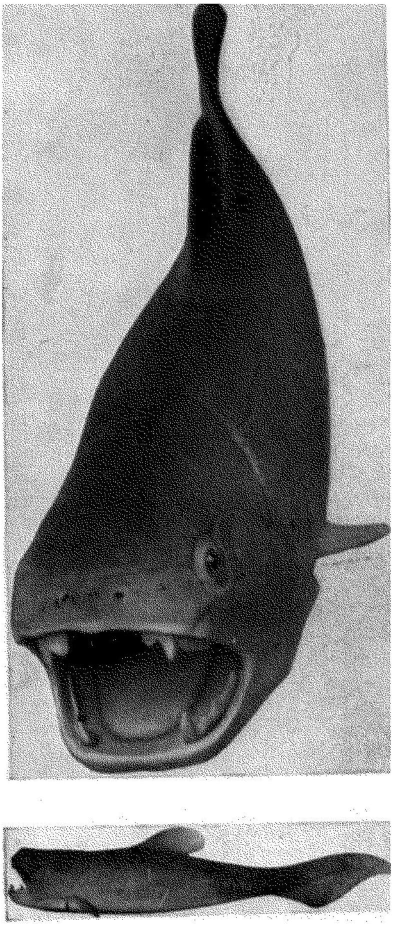

FIG. 12. RESTORATION OF THE GIGANTIC MIDDLE DEVONIAN ARTHRODIRAN (JOINTED NECK) FISH *Dinichthys intermedius*, EIGHT FEET IN LENGTH, OF THE CLEVELAND SHALES (OHIO), showing the bony teeth and bony armature of the head region. Lateral view of the same model in the American Museum of Natural History. Model by Dr. Louis Hussakof and Mr. Horter.

The central line of fish evolution is found in the typical cartilaginous skeleton and jaws and four fins of the primordial sharks, the primitive fusiform stage of which appears in the spine-finned type (Acanthodian) of Upper Silurian time. The relatively large-headed, bottom-living types of sharks do not appear until the Devonian, during which epoch the early swift-moving, fusiform predaceous types branch off into the elongated eel-shaped forms of the Carboniferous. The prototype of the shark group is the *Cladoselache*, a fish famed in the annals of comparative anatomy since it demonstrates that the fins of fishes arise from lateral skin folds of the body with internal stiffening cartilaginous rods (Fig. 13), which in course of evolution are concentrated to form the central axis of a freely jointed fin, while in a further step of evolution they transform into the cartilages and bones of the limb girdles and limb segments of the four-footed land vertebrates (Tetrapoda). The manner of this transformation has been one of the greatest problems in the solution of the origin of animal form since the earliest researches of Carl Gegenbaur of Heidelberg, who sought to derive the lateral fins from modification of the cartilaginous rods supporting the gills, through a profound change of function. While paleontology has disproved Gegenbaur's hypothesis that the limbs of the higher vertebrates, including those of man, are derived from the gill arches of fishes, it has helped to demonstrate the truth of Reichert's hypothesis that the bony chain of the middle ear of man has been derived through change of function from a portion of a modified gill arch (mandibular cartilage) of the fish.

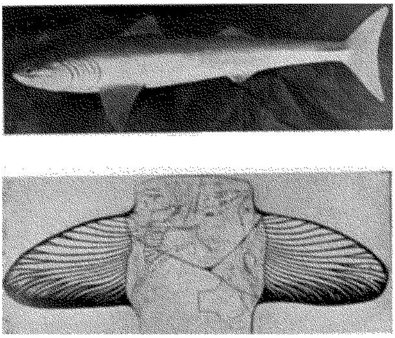

Fig. 13. (Upper.) *Cladosclache*, the Type of the Primitive Devonian Shark of Ohio with Paired and Median Fins Provided with Rod-like Cartilaginous Supports, from which type by fusion the limbs of all the higher land vertebrates have been derived. Model by Dean, Hussakof and Horter from specimens in the American Museum of Natural History.

(Lower.) The Lappet Fins of *Cladoselache* Showing the Cartilaginous Rays (White) Within the Fin (Black). After Dean.

The cycle of shark evolution in course of geologic time embraces a majority of the swift-moving, predaceous types, which branch into the sinuous, elongate body of the frilled shark (*Chlamydoselache*) and into forms with broadly depressed bodies such as the bottom-living skates and rays. Under the law of adaptive radiation the sharks seek every possible habitat zone in the search for food. The nearest approach to the eel-shaped type among the sharks are certain forms discovered in Carboniferous time. By Upper Devonian time the fishes in general had already radiated into all the great existing groups. The primitive armored Arthrodires and Ostracoderms were nearing extinction. The sharks were still in the early lappet-fin stage of evolution above described, a common characteristic of the family being that they never evolved a bony armature. The scaled armature of the first true Ganoid fishes (*Osteolepis, Cheirolepis*) makes its first appearance. These armored knights of the sea are related to simpler forms which gave rise to the rich stock of sturgeons, garpikes, bow-fins, and true bony fishes (Teleosts) which now dominate all other fish groups both in the fresh-waters and the seas. Close to this stock are the first lung fishes (Dipnoi), represented by *Dipterus;* also the "lobe-" or "fringe-finned" Ganoids from which the first land vertebrates were derived. From a single locality, in the Old Red Sandstone of Scotland, Traquair has recovered a whole series of these archaic fish types as they lived together in the fresh water or the brackish pools of Upper Devonian time. (Fig. 14.)

In this period the paleogeographers (Schuchert) obtain their first evidence of the evolution of the terrestrial environment in the indications of the existence of parallel mountain ranges on the British Isles, of active volcanoes in the Gaspé region of New Brunswick, in the mountain formations of South Africa, and in the depressions of the center of the Eurasiatic continent into the great central Mediterranean sea, the *Tethys* of Suess. In the seas of this time as compared with Cambrian seas we observe that the trilobites are in a degenerate phase, the brachiopods are relatively less numerous, the echinoderms are represented by the bottom-living starfishes, the sharks are abundant, the Arthrodiran fishes are still abundant in Germany.

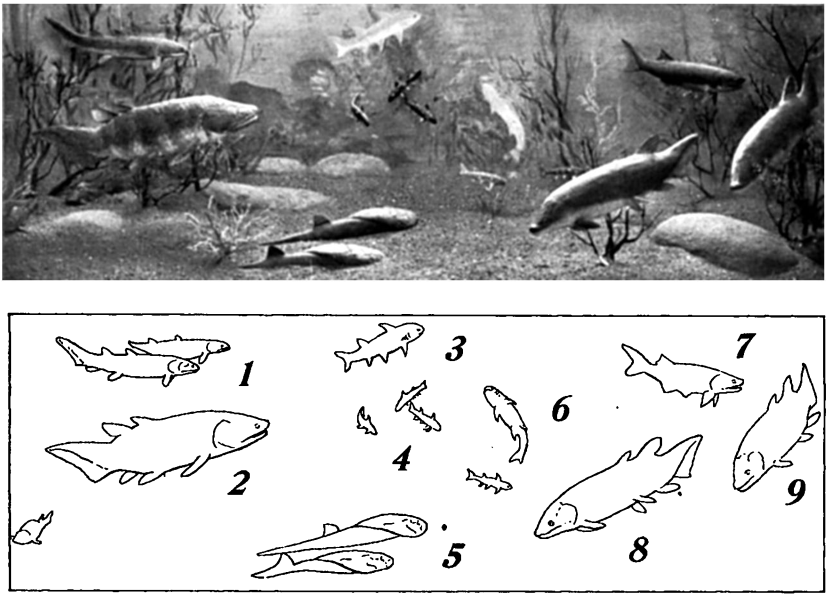

FIG. 14. FISH TYPES OF THE OLD RED SANDSTONE OF SCOTLAND. UPPER DEVONIAN TIME. PRIMITIVE GANOIDS (*Osteolepis, Cheirolepis*), primitive spine-finned sharks, Acanthodians (*Diplacanthus*), bottom-living Ostracoderms (*Pterichthys*), first lung fishes (*Dipterus*), partly armored Ganoids (*Holoptychius*). 1, *Osteolepis*, primitive lobe-finned Ganoid. 2, *Holoptychius*, fringe-finned Ganoid. 3, 6, *Cheiracanthus*, spine-finned shark (Acanthodian). 4, *Diplacanthus*, spine-finned shark (Acanthodian). 5, *Coccosteus* primitive Arthrodiran. 7, *Cheirolepis*, primitive Ganoid. 8, 9, *Dipterus*, primitive lung fish. 10, *Pterichthys*, bottom-living Ostracoderm allied to *Bothriolepis*. Models in the American Museum of Natural History, restorations by Dean, Hussakof and Horter, partly after Traquair.

It was long believed that the Amphibia evolved from the Dipnoi, the air-breathing fishes of the inland fresh waters, and this hypothesis was stoutly maintained by Carl Gegenbaur, who upheld what he termed the Archipterygian theory of the origin of the limb, seeking the prototype of the modern limbed forms in the fin of the modern Australian lung fish, *Ceratodus.* This hypothesis of Gegenbaur, warmly supported by a talented group of his students, is memorable as the last of the great hypotheses regarding vertebrate evolution founded exclusively

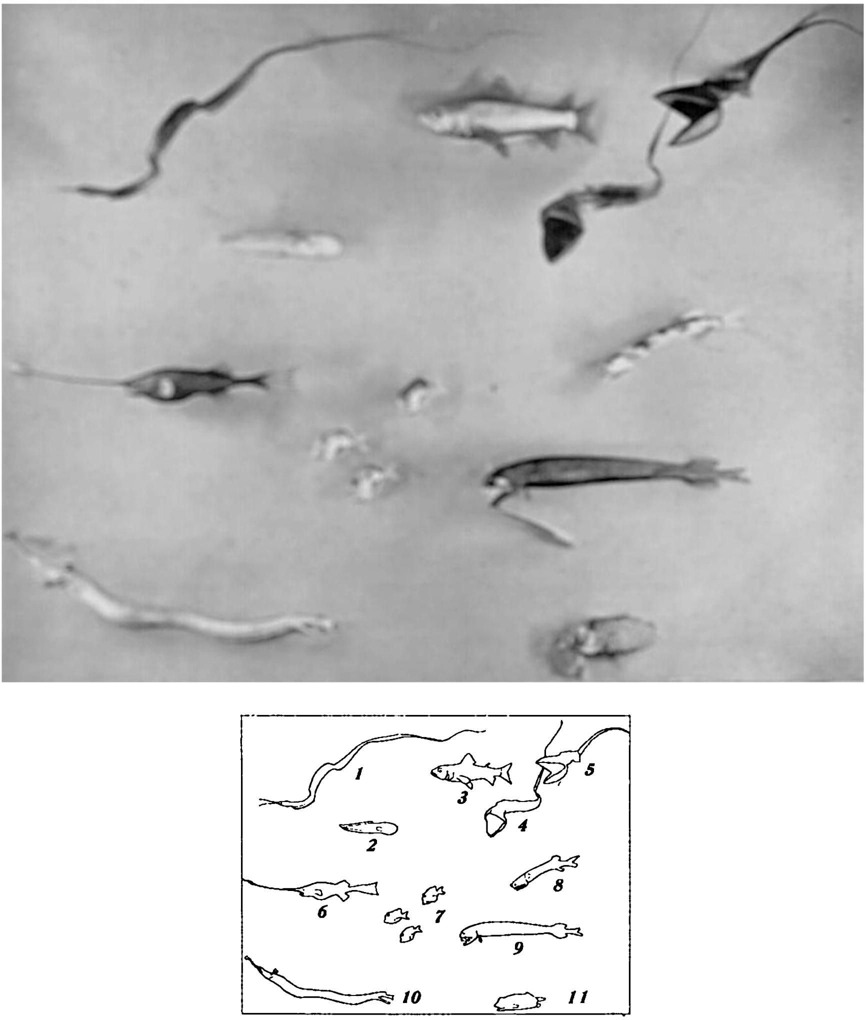

FIG. 15. THE EXTREMES OF ADAPTATION IN MOTION AND ILLUMINATION IN THE EXISTING BONY FISHES (TELEOSTS) OF THE ABYSSAL REGIONS OF THE OCEANS. Although many different orders of Teleosts are represented each type has acquired phosphorescent organs, affording a fine example of convergence. The body form is of great diversity.

1, Thread-eel, ***Nemichthys scolopaceus*** Richardson. 2, ***Barathronus diaphanus*** Brauer. 3, ***Neoscopelus macrolepidotus*** Johnson. 4, 5, ***Gastrostomus bairdi*** Gill and Ryder. 6, ***Gigantactis ranhoeffeni*** Brauer. 7, ***Sternoptyx diaphana*** Lowe. 8, ***Gigantura chuni*** Brauer. 9, ***Melanostomias melanops*** Brauer. 10, ***Stylophthalmus paradoxus*** Brauer. 11, ***Opisthoproctus soleatus*** Vaillant.

upon comparative anatomy and embryology as opposed to the triple evidence afforded by these sciences when reenforced by paleontology.

It is through the discovery of primitive types of the fringe-finned ganoids, to which Huxley gave the appropriate name Crossopterygia, that the true ancestry of the Amphibia and of the amphibian limb has been traced, as due to a partial change of function whereby the propelling fin was gradually transformed into the propelling limb. This implies a long terrestrio-aquatic phase in which the fin was partly used for propulsion on muddy surfaces (Fig. 17). In the parallel retrogressive evolution of the lung fishes (*Lepidosiren, Gymnotus*) the fringe-finned fishes (*Calamoichthys*) and the bony fishes (*Anguilla*) the final eel-shaped, finless stage is either approached or actually passed.

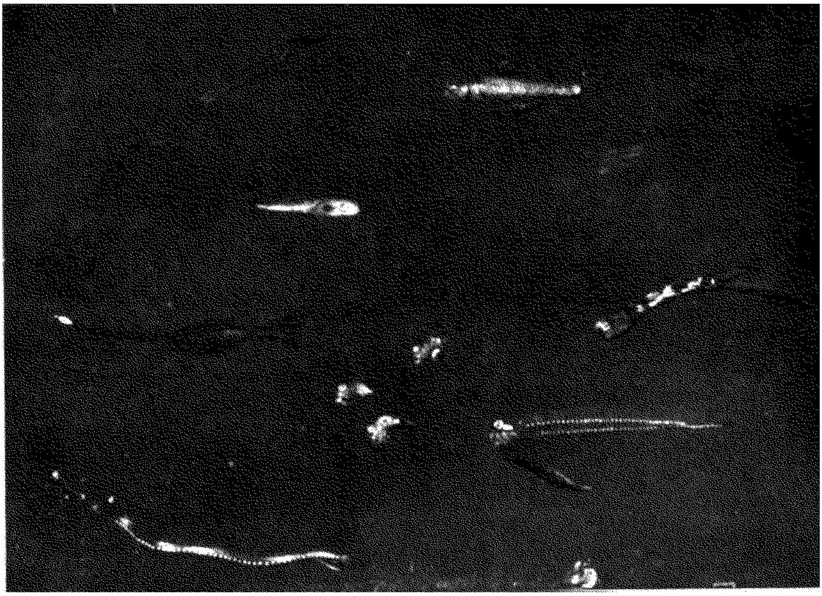

FIG. 16. PHOSPHORESCENT ILLUMINATING ORGANS OF THE ABYSSAL FISHES REPRESENTED IN FIG. 15, as they are supposed to appear in the darkness. After models in the American Museum of Natural History.

The bony fishes (Teleosts), which first emerge as a distinct group in Jurassic time, radiate adaptively into all the great body types attained by the older groups, more or less closely imitating each in turn, so that it is not easy to distinguish superficially between the armored catfishes (*Loricaria*) of the existing South American waters and their prototypes (*Cephalaspis*) of the early Paleozoic. The most extreme specialization in this great group is to be found in the radiations of abyssal fishes into slow- and swift-moving forms inhabiting the great depths of the ocean, adapted to tons of water pressure, to temperatures just above the freezing point, and to total absence of light which is compensated for by the evolution of a great variety of phosphorescent light producing organs.[7] Another extreme of chemical evolution among the fishes is the production of electricity as a protective function, which is even more effective than bony armature because not interfering with rapid motion. In only a few of the fishes is electricity generated in sufficient amounts to thoroughly protect the organism. It develops through modified body tissues in the form of superimposed plates (electroplaxes) separated equally from one another by layers of a peculiar jelly-like connective tissue, all lying parallel to each other and at right angles to the direction of discharge. The electric organ is formed from modified muscle and connective tissue and is innervated by motor nerves. The physical principle involved is that of the concentration cell, and the electrolyte used in the process is probably sodium chloride. The theory is that at the moment of discharge a membrane is formed on one surface of the electroplax which prevents the negative ions from passing through while the positive ions do pass

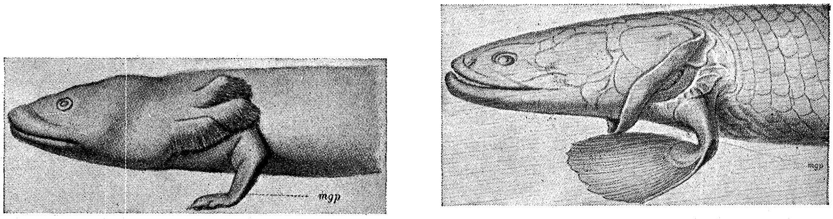

FIG. 17. THEORETIC MODE OF CONVERSION OF THE LOBE-FIN OF THE FISH (RIGHT) INTO THE FOOT OF AN AMPHIBIAN (LEFT) through loss of the dermal fringe border and rearrangement of the cartilaginous supports of the lobe. After Klaatsch.

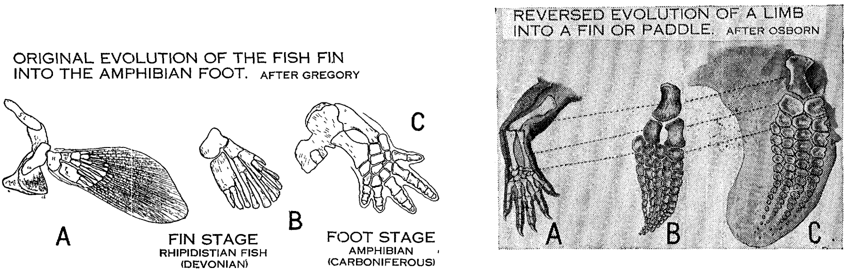
ORIGINAL EVOLUTION OF THE FISH FIN INTO THE AMPHIBIAN FOOT. AFTER GREGORY
A
B
C
FIN STAGE
RHIPIDISTIAN FISH
(DEVONIAN)
FOOT STAGE
AMPHIBIAN
(CARBONIFEROUS)
REVERSED EVOLUTION OF A LIMB INTO A FIN OR PADDLE. AFTER OSBORN
A
B
C

FIG. 18. (LEFT.) DIRECT ORIGINAL EVOLUTION OF THE BONES OF THE LOBE-FIN OF A FISH (*A, B*) (*Rhipidistia* type of Cope) into the bony, five-rayed limb (*C*) of the Amphibian of the Carboniferous age.

(RIGHT.) SECONDARY REVERSED EVOLUTION OF THE FIVE-RAYED LIMB OF A LAND REPTILE (*A*) into the fin, or paddle (*B, C*) of an ichthyosaur.

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[7] The author is especially indebted to Professor Ulric Dahlgren, of Princeton University, for notes upon phosphorescent and electric organs.

through and form the current. The strength of the current varies from four volts in *Mormyrus* up to as much as 250 or more in *Gymnotus,* the electric eel, and consists of a series of shocks discharged 3/1000 of a second apart.

EVOLUTION OF THE AMPHIBIA

A single impression of a three-toed footprint (*Thinopus antiquus*) in the Upper Devonian shales of Pennsylvania constitutes at present the sole paleontologic proof of the period of transition from the fish type to the amphibian type. This took place in Lower Devonian if not in Upper Silurian time. The adaptive radiation of these primordial Amphibia probably began in Middle Devonian time and extended through the great swamp, coal-forming period of the Carboniferous, which afforded over vast areas of the earth's surface ideal conditions for amphibian evolution, the stages of which are best preserved in the Coal Measures of Scotland, Saxony, Bohemia, Ohio and Pennsylvania, and have been revealed through the studies of von Meyer, Owen, Fritsch, Cope, Credner and Moodie. The earliest of these terrestrio-aquatic

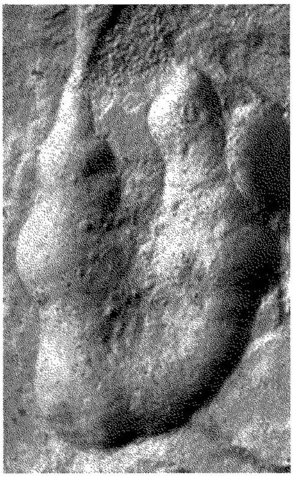

FIG. 19. FOOTPRINT OF *Thinopus antiquus* MARSH, THE EARLIEST KNOWN LIMBED ANIMAL, an Amphibian from the Upper Devonian of Pennsylvania. Type in the Peabody Museum of Yale University. Photograph of cast presented to the American Museum by the Peabody Museum.

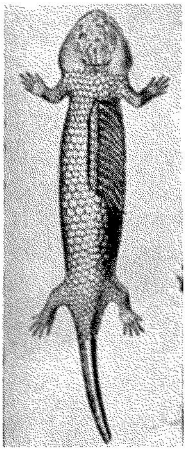

FIG. 20. THE TYPE OF SALAMANDER-LIKE PRIMITIVE AMPHIBIAN OF UPPER DEVONIAN TIME (*Pentadactyloidea, Tetrapoda*), with large, solidly roofed skull, four limbs, and five fingers on each of the fore and hind feet. After Fritsch.

types have not only a dual breathing system of gills and lungs but a dual motor equipment of limbs and a propelling median fin in the tail region.

So far as known primordial Amphibia in body form were chiefly of the small-headed, long-bodied, small-limbed, tail-propelled type of the modern salamander and newt. The large-headed, short-bodied types (*Amphibamus, Pterophlax*) were primitive. In Upper Carboniferous and early Permian time the terrestrial forms began to be favored by the land elevation and recession of the sea which distinguished the close of the Carboniferous and early Permian time. Under these varied zonal conditions, aquatic, palustral, terrestrio-aquatic, fossorial and terrestrial, the Amphibia radiated into several habitat zones and adaptive phases, thus recapitulating all the chief types of body form which had previously evolved among the fishes and anticipating many of the types of body form which were to evolve among the Reptilia. One ancestral feature is a layer of superficial body scales derived from those of their

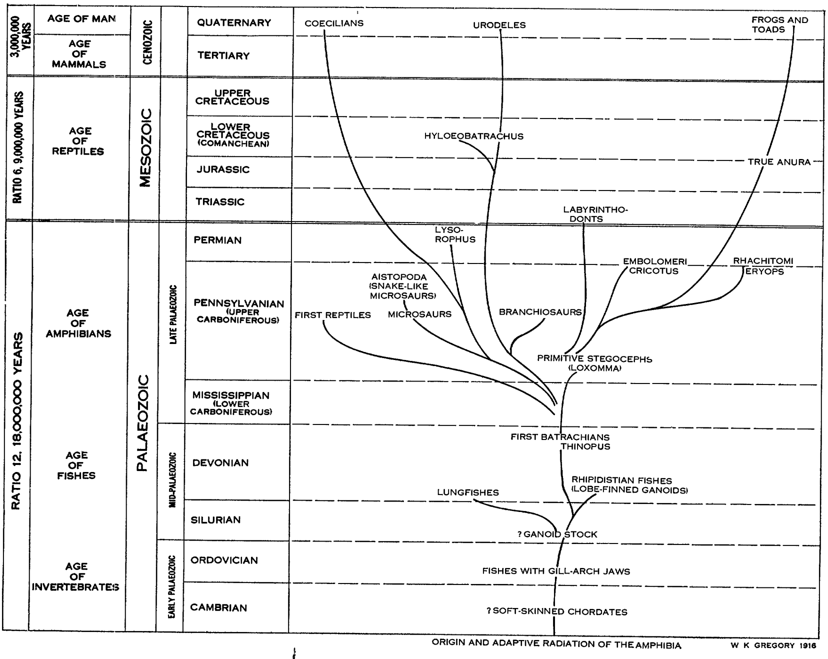

FIG. 21. DESCENT OF THE AMPHIBIA IN WHICH THE FIN IS TRANSFORMED INTO A LIMB (*Thinopus*), from an ancestral Ganoid fish stock of Silurian age through the fringe-finned Ganoids. From this group diverge the ancestors of the Reptilia and the salamander-like Amphibians which give rise to the various salamander types, also to branches of limbless and snake-like forms (*Aistopoda,* modern Cœcilians). The other great branch of the solid-skulled Amphibia, the Stegocephala, was widespread all over the northern continents in Permian and Triassic time (*Cricotus, Eryops*), and from this stock descended the modern frogs and toads (*Anura*). Prepared for the author by Wm. K. Gregory.

fringe-finned fish ancestors; with the loss of these scales most of the Amphibia also lost the power of forming a bony dermal armature.

Recent researches in this country, chiefly by Williston and Case, indicate that the solid-headed Amphibia (Stegocephala) and primary forms of the Reptilia chiefly belong to late Carboniferous (Pennsylvania) and early Permian time. They are found abundantly in pool deposits widespread over the southwestern United States and Europe associated in rocks of a reddish color, which point to aridity of climate in the northern hemisphere during the period in which the terrestrial adaptive radiation of the Amphibia occurred. These arid conditions continued during the greater part of Permian time, especially in the northern hemisphere. In the southern hemisphere there is evidence even of a period of extensive glaciation, which was accompanied by the disappearance of the old lycopod flora (club mosses) and arrival of the cool fern flora (*Glossopteris*) which appeared simultaneously in South America, South Africa, Australia, Tasmania and southern India. The widespread distribution of this flora in the southern hemisphere furnishes one of the arguments for the existence of the great South Pacific continent *Gondwana*, a hypothesis of Suess which is supported by Schuchert. In North America Permian glaciation was only local. The last of the great Paleozoic seas disappeared from the surface of the continents, while the border seas give evidence of the rise of the ammonite cephalopods. Toward the close of Permian time the continent was completely drained. Along the eastern seaboard the Appalachian revolution occurred, and the mountains rose to heights estimated at from three to five miles.

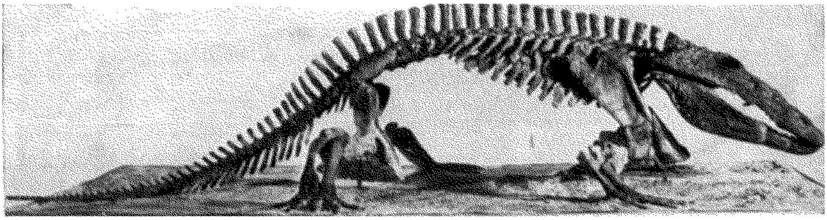

FIG. 22. SKELETON OF *Eryops* FROM THE PERMO-CARBONIFEROUS OF TEXAS, type of the stegocephalian Amphibians which were structurally ancestral to the Labyrinthodonts of the Triassic. Mounted in the American Museum of Natural History.

Evidences of extensive continental connections in the northern hemisphere are found in the community of type between the great terrestrial amphibians of such widely separated areas as Texas and Württemberg which develop into similar resemblances between the great Labyrinthodont amphibians of Lower Triassic times of Europe, North America and Africa. Ancestral to these Triassic giants is the large, sluggish, water- and shore-living *Eryops* of the Texas Permian, with massive head, depending on its short, powerful limbs and broad, spreading feet for land propulsion and in a less degree upon its tail for propulsion in the water. This form may be a collateral ancestor of the Labyrinthodonts; it belongs to a type which spread all over Europe and North America and persisted into the *Metopias* of the Triassic.

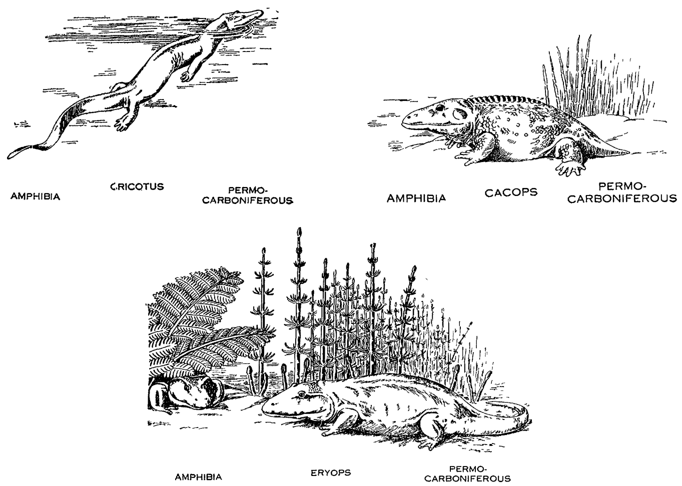

FIG. 23. AMPHIBIA OF THE AMERICAN PERMO-CARBONIFEROUS, the free-swimming *Cricotus*, short-bodied *Caccops*, and continuation of the amphibious short-tailed terrestrial type, the large, solid-headed *Eryops*. Restorations for the author by Gregory and Deckert.

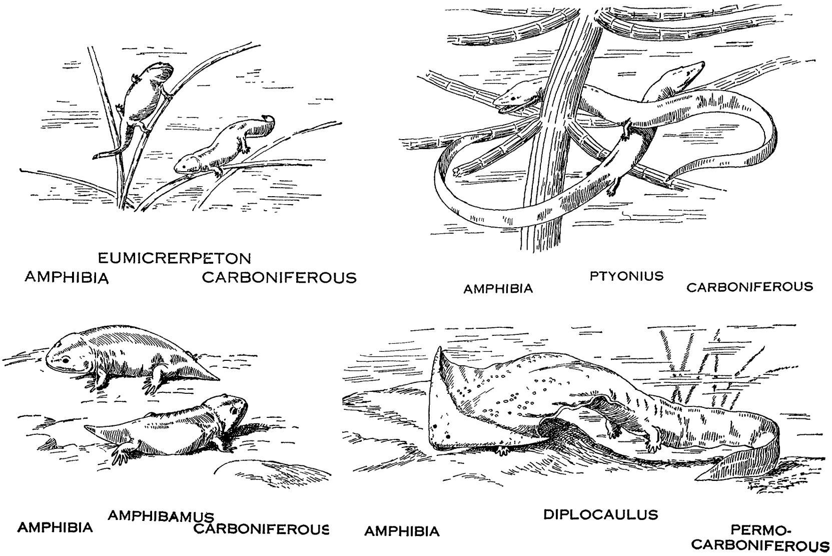

FIG. 24. CHIEF AMPHIBIAN TYPES OF THE CARBONIFEROUS, the early short-tailed, land-living *Amphibamus*, the salamander-like *Eumicrerpeton*, the eel-bodied *Ptyonius*, the broad-headed, bottom-living *Diplocaulus*. Restorations for the author by Gregory and Deckert.

An opposite extreme of slender body structure is found in the active predaceous types of water-loving amphibians such as *Cricotus*, of rapid movements, propelled by a long tail fin and with sharp teeth adapted to seizing an actively moving prey. This type retrogresses into the eel-like, bottom-loving *Lysorophus* with its slender skull, elongate body propelled by lateral swimming undulations, the limbs relatively useless. Corresponding to the bottom-living fishes are the large, sluggish, broad-headed, bottom-living amphibians, such as *Diplocaulus*, with heads heavily armored, limbs small and weak, the body propelled by lateral motions of the tail. There were also more powerful, slow-moving, long-headed, alligator-like, terrestrio-aquatic forms, such as the *Archegosaurus* of Europe and the fully aquatic *Trimerorachis* of America. An extreme stage of terrestrial, ground-living evolution with marked reduction of the use of the tail for propulsion is the large-headed *Caccops*, short-bodied, with limbs of medium size, but with feeble powers of prehension in the feet. Radiating around these animals were a number of terrestrial types exhibiting the evolution of dorsal protective armature and spines (*Aspidosaurus*); other types lead into the pointed-headed structure and pointed teeth of *Trematops*.

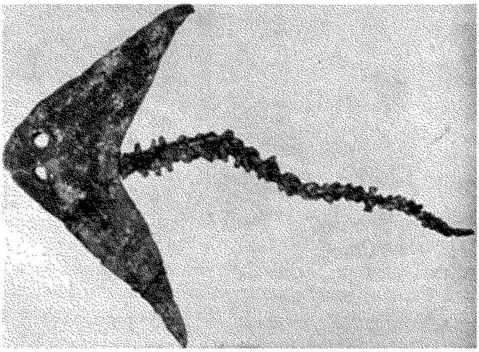

FIG. 25. SKULL AND VERTEBRAL COLUMN OF *Diplocaulus*, a typical solid-, broad-headed Amphibian from the Permian of northern Texas. Specimen in the American Museum of Natural History.

Editorial Note: The remaining parts of this Lecture will appear in December or January in book form under the title "Origin and Evolution of Life," from the press of Charles Scribner's Sons.